

# H I L G A R D I A

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## CHARACTERS, DISTRIBUTION, AND FOOD PLANTS OF LEAFHOPPER VECTORS OF VIRUS CAUSING PIERCE'S DISEASE OF GRAPEVINES<sup>1</sup>

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### INTRODUCTION

PIERCE'S DISEASE OF GRAPEVINES, now widespread and destructive in California vineyards, has been under study by a number of investigators at this experiment station since 1934. In 1936 the cause was found to be a virus, transmissible by grafts and cuttings (Hewitt, 1941).<sup>4</sup> The virus was later reported (Hewitt, Houston, Frazier, and Freitag, 1946) to be identical with that causing alfalfa dwarf.

Leafhopper transmission of the virus was first demonstrated by Hewitt, Frazier, and Houston (1942) and by Houston, Frazier, and Hewitt (1942). Since then leafhoppers have been reported as vectors by Hewitt, Frazier, Jacob, and Freitag (1942); Frazier (1944); Frazier and Freitag (1946); and Hewitt, Houston, Frazier, and Freitag (1946). A total of fourteen species have been reported, as follows:

*Carneocephala fulgida* Nottingham  
*Carneocephala triguttata* Nottingham  
*Cuerna occidentalis* Oman and Beamer  
*Draeculacephala minerva* Ball  
*Friscanus friscanus* (Ball)  
*Helochara delta* Oman  
*Neokolla circellata* (Baker)

*Neokolla confluens* (Uhler)  
*Neokolla hieroglyphica* (Say)  
*Neokolla severini* DeLong<sup>5</sup>  
*Pagaronia confusa* Oman  
*Pagaronia furcata* Oman  
*Pagaronia 13-punctata* Ball  
*Pagaronia triunata* Ball

These leafhoppers, commonly called sharpshooters, all belong to the subfamily Tettigoniellinae (DeLong and Knull, 1945) [= Cicadellinae (Van Duzee, 1916, 1917a; DeLong and Caldwell, 1937) = Amblycephalinae (China, 1939; Medler, 1942)].

In an effort to learn more about the vectors and their relation to the disease, biological and transmission studies were begun in 1942 on nine of the species listed and on a variety of one other. The present paper describes distinctive characters to facilitate identification of vectors, summarizes geographic dis-

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<sup>4</sup> See "Literature Cited" for citations, referred to in the text by author and date.

<sup>5</sup> Until recently, misidentified as *Neokolla gothica*; see page 179.

tribution as given in the literature, and reports new localities and food plants observed in California.

Companion papers (Severin 1949*a, b*) report the life history of one species, *Neokolla circellata*, and transmission experiments with nine of the vectors described in this paper. Eight of the vectors described in the present paper are shown in color in the third paper of this issue.

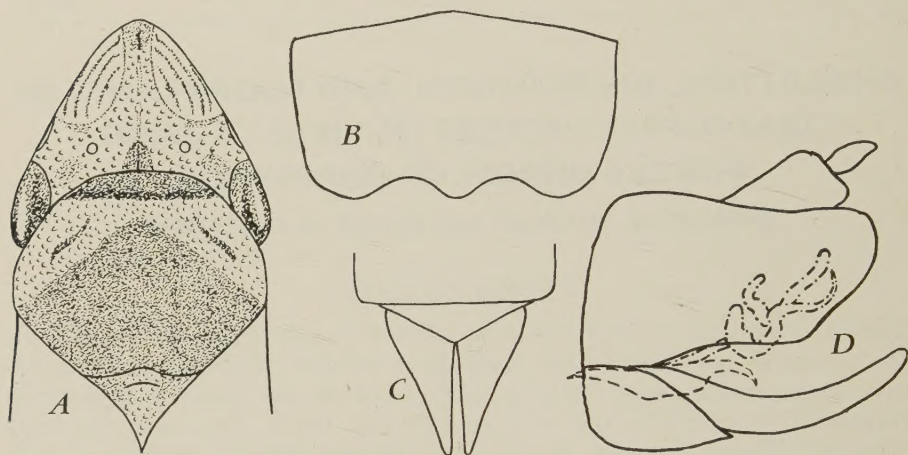


Fig. 1. *Helochara delta* Oman: A, dorsal view of head, pronotum, and scutellum; B, ventral view of female seventh sternite; C, ventral view of male valve and plates; D, lateral view of male genital structures.

### HELOCHARA DELTA

**Characters.** *Helochara delta* Oman was described by Oman (1943) as distinct from *H. communis* Fitch, which it closely resembles in form, appearance, and genitalic structures. It is from 5 to 6 mm in length.

The vertex (fig. 1, A) is more produced than in *Helochara communis*; it is bluntly pointed and almost as long as the pronotum. The width of the vertex between the eyes is almost one fourth greater than its median length.

The color is dark green marked with paler green or yellowish green. The apex of the vertex and the four arcs on the anterolateral margin are black or dark brown. The face is pale dull green to brown.

The posterior margin of the female seventh sternite (fig. 1, B) is broadly concavely emarginate either side of a median produced portion, so that the segment appears trilobate. The male plates (fig. 1, C) are rather short, triangular with acute apices. The styles (fig. 1, D) are rather broad at the base, narrowed rather abruptly on the outer margin at about three fourths their length and produced to form an apical fingerlike process, which curves outward and is pointed on the outer margin at the apex. The aedeagus is about uniform in size throughout, and two pairs of lateral processes arise near the base. The pair at the basal end are short and extend dorsally. The other pair are narrow, curved across the aedeagus and usually extend to its apex.

**Distribution and California Food Plants.** *Helochara delta* is known from California only. Oman (1943) records the type locality of *Helochara delta*

from General Grant Park, California, elevation 6,500 feet, October 16, 1941. Other specimens are from Kenwood and Smith River, California.

N. W. Frazier collected a large population of *Helochara delta* on reed grasses (*Calamagrostis* sp.), rush grasses (*Juncus* sp.), and species of *Cyperus* growing in bogs at Kenwood, California, on September 25, 1943.

A mixed population of *Helochara delta* and *Carneocephala fulgida* was collected on Sudan grass (*Sorghum vulgare* var. *sudanense*), near Geyserville, Sonoma County, on September 6, 1946.

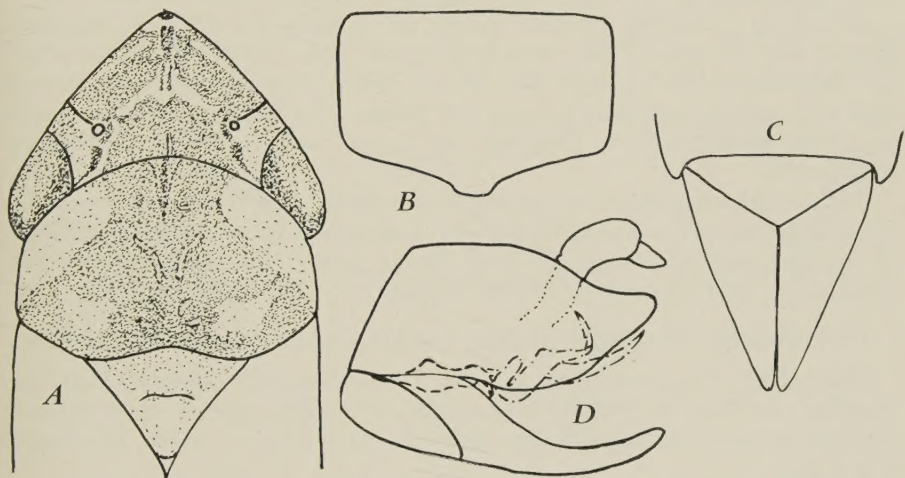


Fig. 2. Redheaded sharpshooter, *Carneocephala fulgida* Nottingham: A, dorsal view of head, pronotum, and scutellum; B, ventral view of female seventh sternite; C, ventral view of male valve and plates; D, lateral view of male genital structures.

## THE REDHEADED SHARPSHOOTER, CARNEOCEPHALA FULGIDA

**Characters.** In general appearance *Carneocephala fulgida* Nottingham closely resembles *C. flaviceps* (Riley) but is darker green and has a more pointed head. The male is smaller, 4.5 to 5.0 mm long, while the female is 5.5 to 6.0 mm long. The species was described by Nottingham in 1932.

The vertex (fig. 2, A) is rather flat and granulated. The width between the eyes is about one and one half times as great as the median length. The apex is pointed. The pronotum is about one third longer than the vertex.

The color of the vertex of the male is usually a little darker than that of the female. In each case the vertex is fulvous with paler spots. There is a pale spot at the apex, spots around the ocelli, a pale arc connecting them, and a spot anterior to the arc. There are pale bands along the anterior margin, and the posterior margin is greenish yellow. The pronotum and scutellum are yellowish green. The elytra are dark green with paler veins, and the apices are smoky. The face is pale brownish, mottled with paler spots.

The posterior margin of the female seventh sternite (fig. 2, B) is broadly and slightly produced at the middle and slightly sinuate on either side.

The male plates (fig. 2, C) are triangular, rather broad at the base, the apices acute and blunt, each with a fingerlike process. The styles are rather

short and tapered from the base to a pointed apex. In lateral view (fig. 2, *D*) the aedeagus is short and curved, with two pairs of lateral processes arising ventrally. The basal pair are shorter, the second pair longer; and the tips of the processes are curved dorsally and caudally.

**Geographical Distribution and California Food Plants.** Records indicate that the redheaded sharpshooter is known only from California. Nottingham (1932) notes the following localities for it: Lemon Cove, July 24, 1929 (R. H. Beamer); Winters, August 6, 1929 (R. H. Beamer); Sacramento, August 7, 1929 (L. D. Anderson); and Spreckels, May 14, 1929 (G. E. Bense).

According to Hewitt, Frazier, Jacob, and Freitag (1942), *Carneiocephala fulgida* has in general been found under the same conditions as described for *Draeculacephala minerva* but favors open and exposed soils which support low, sparsely growing grasses and weeds. This leafhopper is commonly found on puncture vine (*Tribulus terrestris*) and cocklebur (*Xanthium canadense*).

*Carneiocephala fulgida* was collected on grasses and weeds growing in the dry stream bed of the Russian River near Larkmead. An enormous population of nymphs and adults occurred on Sudan grass (*Sorghum vulgare* var. *sudanense*) near Geyserville, Sonoma County, on September 6, 1946.

### THE GREEN SHARPSHOOTER, *DRAECULACEPHALA MINERVA*

**Characters.** The green sharpshooter, *Draeculacephala minerva* Ball, was described by Ball in 1927. It is the common western species of dark green and yellow grass leafhopper. The male is 6 to 7 mm. in length, the female 7 to 9 mm.

The vertex (fig. 3, *A*) is bluntly angled. In both sexes its width between the eyes at the base is a little greater than its median length. The margins are convexly rounded to a blunt-pointed apex.

The color of the vertex, the anterior half of the pronotum, and the scutellum is yellow. There is a conspicuous brown spot on the apex of the vertex and a black impressed line from the margin to the ocellus. Along the margin on either side there are three conspicuous parallel brown arcs. The posterior half of the pronotum is dark green. The elytra are dark green with pale veins.

The posterior margin of the female seventh sternite (fig. 3, *B*) is broadly, angularly notched on either side of the middle to form a broad, bluntly angled, produced, median tooth, and lateral angles which are slightly produced.

The male plates (fig. 3, *C*) are elongate, triangular, exceeded in length by the pygofer. The aedeagus (fig. 3, *D, E, F*) possesses a ventro-anterior portion from which a pair of processes extend dorsally. The dorso-posterior portion has a pair of long processes at the base which are vermiculate and longer than the aedeagus, extending dorsally and caudally. The ventral process is deeply constricted near the base, then curved to form a rounded spoon-shaped portion with the apex, which is broadly rounded.

**Geographical Distribution and California Food Plants.** This species is western and southwestern in distribution. It has been collected in California, Oregon, Nevada, Utah, Arizona, New Mexico, Texas, Mexico, Guatemala, and the Canal Zone.

Ball (1927) gives the following localities for the green sharpshooter in California: Stanford, June 21, 1908 (Ball); San Jose (King); and Chino (Ball and Titus).

According to Hewitt, Frazier, Jacob, and Freitag (1942), the green sharpshooter is widely distributed in California. It is commonly found in moist situations, as in marshes and bogs, along streams and ditches, and in wet areas created by irrigation practices. Well-irrigated alfalfa fields which have a thinning stand of plants contain certain plants that provide situations for

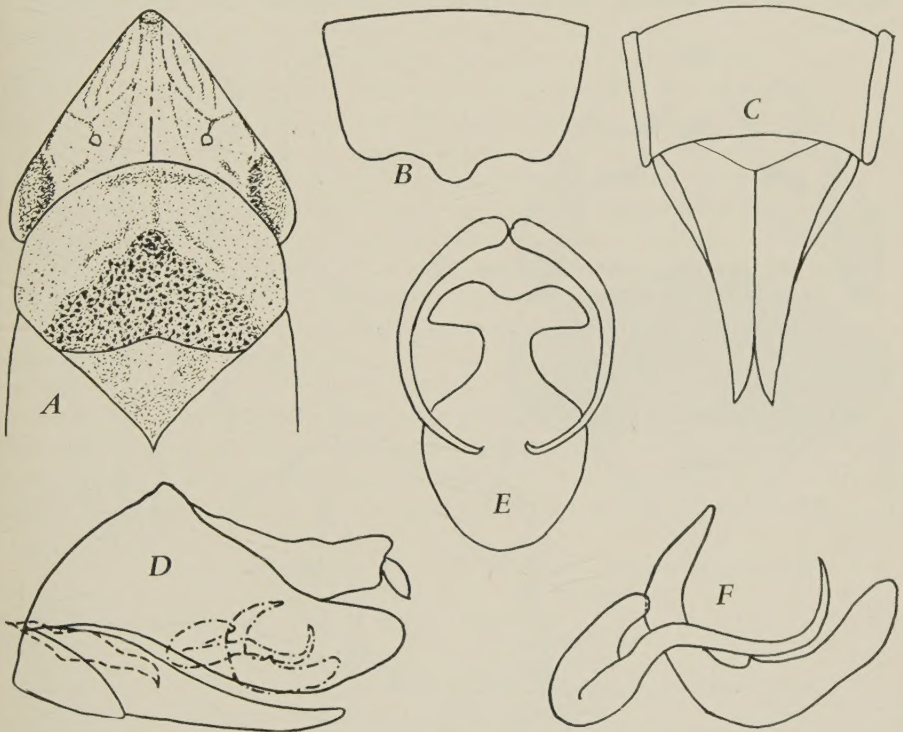


Fig. 3. Green sharpshooter, *Draeculacephala minerva* Ball: A, dorsal view of head, pronotum, and scutellum; B, ventral view of female seventh sternite; C, ventral view of male plates; D, lateral view of male genital structures; E, ventral view of male aedeagus; F, lateral view of male aedeagus.

large numbers of this leafhopper. Populations of this leafhopper have also been observed in young grain fields, in orchard covercrops, in uncultivated areas around buildings, on lawns, along roadsides, railroad right-of-ways, irrigation ditches, and canals, and in permanent pastures. Grasses afford preferred food and breeding plants, Bermuda grass (*Cynodon dactylon*) being especially favored. The leafhopper is common on puncture vine (*Tribulus terrestris*) and on cocklebur (*Xanthium canadense*).

The source of supply of *Draeculacephala minerva* for experimental purposes was on grasses in a depleted alfalfa field near Milpitas, Santa Clara County, and along the margins of a bog at Sharp Park, San Mateo County.

The leafhopper was collected in many other localities in the coastal fog belt, and in the Salinas, San Joaquin, Sacramento, and Napa valleys.

### THE BLUE-GREEN SHARPSHOOTER, *NEOKOLLA CIRCELLATA*

**Characters.** The blue-green sharpshooter, *Neokolla circellata* (Baker), was described by Baker in 1898 as a member of *Tettigonia*. *T. circellata* was a manuscript name used by Uhler but not published. For many years this species was placed as a synonym of *Tettigonia atropunctata* Signoret but has recently been recognized as an apparently good species. The length is 6 to 7 mm.

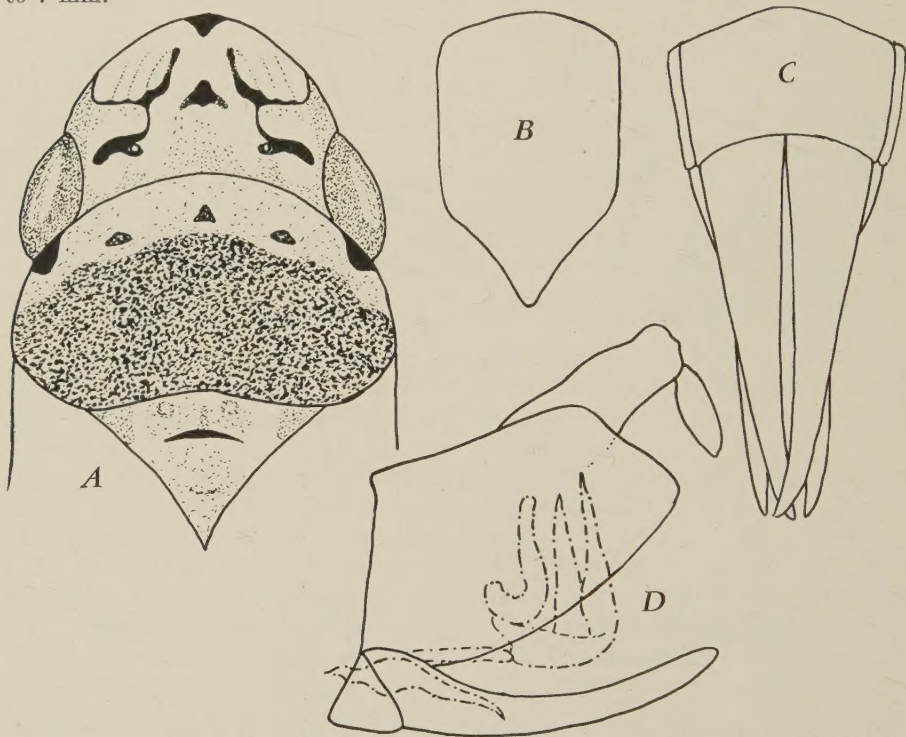


Fig. 4. Blue-green sharpshooter, *Neokolla circellata* (Baker): A, dorsal view of head, pronotum, and scutellum; B, ventral view of female seventh sternite; C, ventral view of male valve and plates; D, lateral view of male genital structures.

The vertex (fig. 4, A) is blunt, with the sides convexly rounded. It is about one and one third times as wide between the eyes as the median length.

The vertex is yellow in color with a black spot at the apex. There is a spot at the middle, an oblique dash against each ocellus on the outside, and a curved black line on each side along the line of the frontal suture. The pronotum is pale on the anterior half; the posterior half is darker with a series of spots on the anterior portion. The elytra are blue.

The posterior margin of the female seventh sternite (fig. 4, B) is strongly, angularly produced. The median line is keeled; the apex appears pointed because of this keel.

The male plates (fig. 4, C) are long and slender, about four times as long as the basal width. The styles are rather long, narrowed on the apical half to a pointed apex, which curves outward. The aedeagus in lateral view (fig. 4, D) is composed of three erect processes. The apical one is the longest and is sharp-pointed at the apex. The process adjacent to it is a little shorter and is sharp-pointed. The basal process has a shorter anterior and a longer posterior portion, both of which are blunt.

**Geographical Distribution and California Food Plants.** The blue-green sharpshooter is known to occur in Arizona and California.

Baker (1898) records the species from Los Angeles (Koebele).

Hewitt, Frazier, Jacob, and Freitag (1942) state that it is often very common and abundant in the coastal fog belt, especially in canyons and along streams and in valleys. In the San Joaquin Valley it is sometimes found in large numbers, but usually fairly closely confined to stream banks.

This sharpshooter is found on many host plants, but prefers vines, shrubs, trees, and perennial herbs (Hewitt, Frazier, Jacob, and Freitag, 1942). Wild grapevines, wild blackberry, elderberry, and willow are especially common host plants. Grasses and weeds are less commonly infested.

In Berkeley this species frequently completes the nymphal stages on deciduous plants such as Japanese or Boston ivy (*Parthenocissus tricuspidata*), and the adults fly to other food plants during the autumn. Near Larkmead, when the leaves of grapevines began to dry and drop, the adults were abundant on Persian walnut (*Juglans regia*) partly surrounding a vineyard. This sharpshooter completes its nymphal stages on the following plants (those plants which serve only as food plants during the winter are not listed):

Apocynaceae:

*Vinca major*, large periwinkle

Araliaceae:

*Hedera canariensis*, ivy

Compositae:

*Artemisia vulgaris*, California mugwort

Geraniaceae:

*Pelargonium capitatum*

*Pelargonium domesticum*, Lady

Washington geranium

*Pelargonium hortorum*, fish geranium

*Pelargonium peltatum*, ivy geranium

Labiatae:

*Salvia leucantha*

Leguminosae:

*Acacia longifolia*, Sydney golden wattle

Myoporaceae:

*Myoporum laetum*

Myrtaceae:

*Eugenia paniculata* var. *australis*  
(*E. myrtifolia*)

Onagraceae:

*Fuchsia hybrida*

Plumbaginaceae:

*Limonium perezii* (*Statice perezii*)

Pittosporaceae:

*Pittosporum eugenioides*, tarata

Rubiaceae:

*Coprosma baueri*

Saxifragaceae:

*Francoa sonchifolia*

Solanaceae:

*Cestrum purpureum* (*C. elegans*)

Vitaceae:

*Parthenocissus tricuspidata*

## NEOKOLLA CONFLUENS VAR. PACIFICA N. VAR.

**Characters.** *Neokolla confluens* var. *pacifica* resembles *confluens* in general form and appearance, but the genitalia of the male are different. The length is 6.5 to 7.0 mm.

The vertex (fig. 5, A) is bluntly produced, almost twice as broad between the eyes as the median length. The pronotum is about one half longer than the vertex.

The color is gray to cream. The vertex is marked with a heavy black elongated bar extending from either side of the pale apex to near the eye (fig. 5, *A*). The portion next to the eyes is narrowed and is in line with a small spot between its terminus and the eye. There is a heavy bent band either side extending from the base anteriorly through the ocellus, then curved inwardly extending almost to the middle line where it turns abruptly caudally and extends almost to the base. These marks form a median white band from the apex to the base. There is a longitudinal bar which is between the eye and the ocellus. The pronotum is mottled with small darker spots. The scutellum is mostly black with two median anterior pale circular spots, each of which contains a black dot at the center. There is a medium elongate white spot

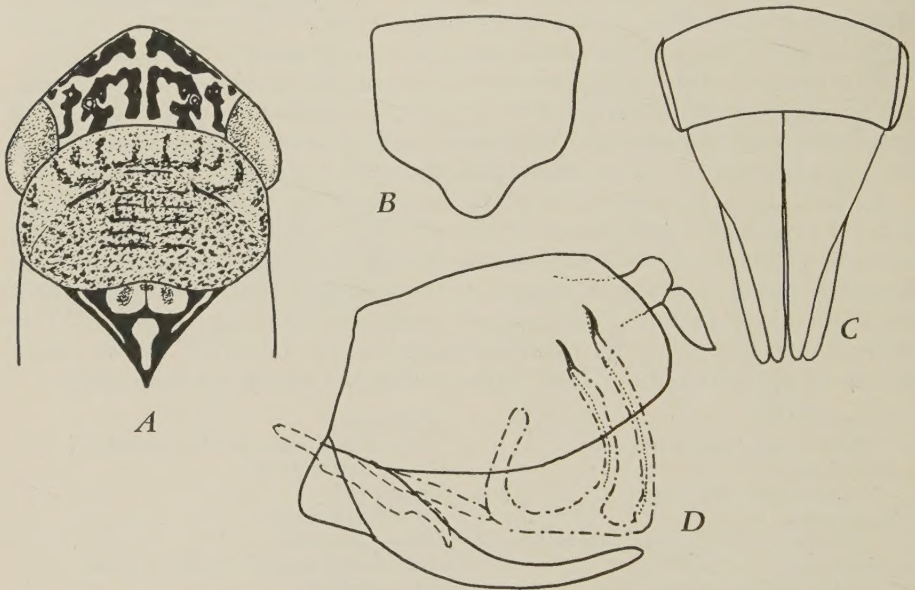


Fig. 5. *Neokolla confluens* var. *pacifica* n. var.: *A*, dorsal view of head, pronotum, and scutellum; *B*, ventral view of female seventh sternite; *C*, ventral view of male valve and plates; *D*, lateral view of male genital structures.

between these and the apex, and a narrow pale diagonal line extending from each basal angle more than half way to the apex just inside the lateral margins.

The posterior margin of the female seventh sternite (fig. 5, *B*) is convexly rounded on the lateral angles, then concavely sloping to form a produced median blunt apex.

The male plates (fig. 5, *C*) are elongate, triangular, each almost three times as long as its basal width, and concavely tapered to a blunt apex. The styles are gradually narrowed from a rather broad base to a narrow apex, which is truncate with a projecting tooth on the outer apical margin. The aedeagus (fig. 5, *D*) is curved upward at the base and has two long, dorsally directed processes, one at the apex of the ventral portion and the other at about the middle of the ventral portion. These are slender and are enlarged and convexly curved on the caudal margin just before the narrow acutely pointed tip.

**Geographical Distribution and California Food Plants.** This variety is known to occur in California and probably in southern Idaho.

During the past four summers, *Neokolla confluens* var. *pacifica* was collected, on rare occasions, on common periwinkle or running myrtle (*Vinca minor*) growing along the banks of the Russian River near Larkmead.

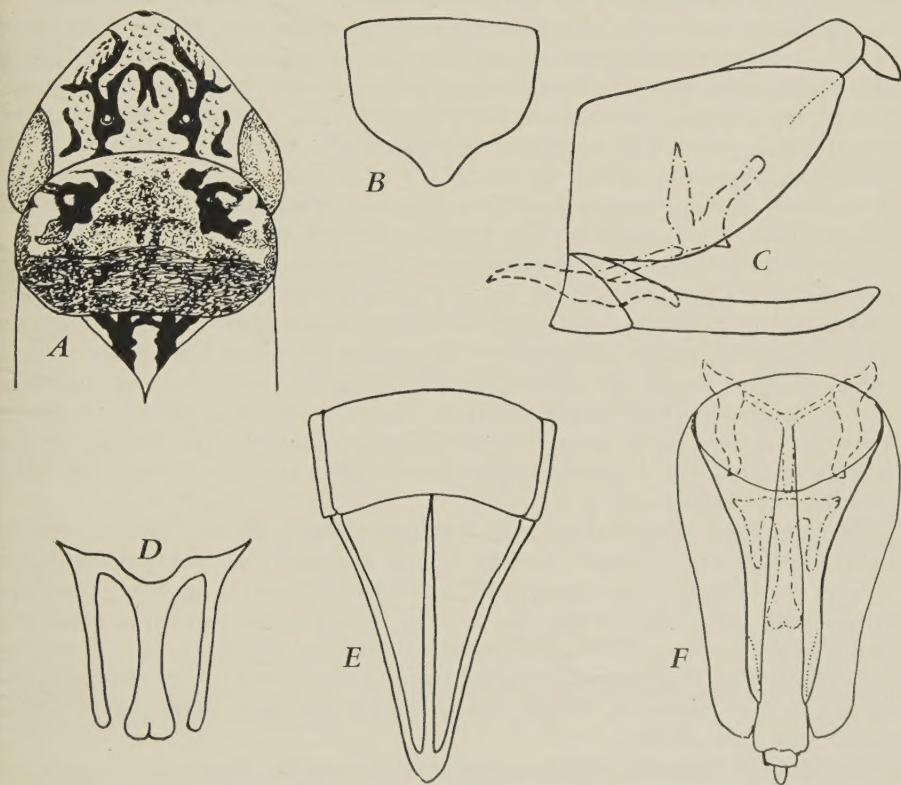


Fig. 6. *Neokolla severini* DeLong: A, dorsal view of head, pronotum, and scutellum; B, ventral view of female seventh sternite; C, lateral view of male genital structures; D, caudal view of male aedeagus; E, ventral view of male valve and plates; F, ventral view of male genital structures. (A, C, D, and F from DeLong, 1948.)

R. Flock collected this variety at Covina (San Dimas Canyon), Los Angeles County, on *Adenostoma*; at Peralta, Orange County; and at Rivera, Los Angeles County.

### NEOKOLLA SEVERINI

**Characters.** *Neokolla severini* DeLong was described in 1948. It had previously been confused with *N. gothica*, which it resembles in color and general appearance. The species occurring in California had been identified as *N. gothica* for many years, but can be distinguished from the latter by the smaller size (5.5 to 6.0 mm long), shorter head, and different male genital structures.

The vertex (fig. 6, A) is produced, bluntly angled, one third wider between the eyes than the median length, and shorter than the pronotum.

The color is somewhat variable. The vertex ground color is grayish, often tinted with red. There is a black spot at the apex (fig. 6, *A*). There is an area on each margin about halfway between the apex and the eye separated from the disk by a black line, which encloses several dark arc-like lines. A black line extends from the inner basal margin of this area to the ocellus, which is enclosed in a black ring. A black line extends forward from the ocellus, curves on the disk to meet the curved line from the opposite side, from which point they are directed basally for a short distance as contiguous lines. There is also a black dash near the base on either side between the ocellus and the eye. The anterior third of the pronotum is pale with black markings. The posterior two thirds is black. The scutellum is gray, often tinted with red, with black lines extending from about the middle of either side to the pronotum. The elytra are usually dark with a few pale markings, and the veins are inconspicuous, often obscured. The face is pale with traces of faint arcs.

The posterior margin of the female seventh sternite (fig. 6, *B*) is strongly angularly produced to a blunt apex. The entire segment is long. The male plates (fig. 6, *E*) are elongate and concavely narrowed on the inner margins to form narrow, rather blunt apices. The plates are about four times as long as the width of each at the base. The styles are rather short, broad at the base, and curved inward to form a blunt apex. The aedeagus is simple and in caudal view (fig. 6, *D*) has an apex which is slightly enlarged and notched at the middle to form two rounded apical lobes. There are two dorsally directed processes at the base (fig. 6, *C*).

**Geographical Distribution and California Food Plants.** The records at hand indicate that *Neokolla severini* occurs in California and is the common species in Arizona. The species was collected by Severin in small numbers on common periwinkle or running myrtle (*Vinca minor*) growing along the banks of the Russian River near Larkmead. Most of the adults used in testing the efficiency of this vector in transmitting the virus causing Pierce's disease of grapevines (Severin, 1949*b*) were reared on large periwinkle (*Vinca major*) by J. H. Freitag.

R. Flock collected *Neokolla severini* at Riverside, Riverside County, on *Ribes* and *Lonicera hispidula* (*L. subspicata*); Berkeley, Alameda County; Covina (San Dimas Canyon), Los Angeles County; East Highlands, San Bernardino County, on *Eriodictyon*; in the San Bernardino Mountains on *Artemisia vulgaris*; and in the San Jacinto Mountains on *Ceanothus*.

### PAGARONIA CONFUSA

**Characters.** *Pagaronia confusa* Oman was described by Oman in 1938. Previously it had been confused with *P. 13-punctata*, which it closely resembles in coloration. It can be separated from *P. 13-punctata* by the broader male plates and the straight lateral processes of the aedeagus (compare fig. 7, *C*, *D*, and fig. 8, *B*, *C*). *P. confusa* is 8.0 to 9.5 mm long.

The vertex of *Pagaronia confusa* (fig. 7, *A*) is a little more pointed than in *P. 13-punctata* (fig. 8, *A*). The length of the vertex on the median line is slightly less than its width between the eyes.

The general color is pale green. It may have the 13 black spots on the head and pronotum as are found on *Pagaronia 13-punctata*, but the spots below

the ocelli and the lateral spots on the pronotum are usually absent (Oman, 1938).

The posterior margin of the female seventh sternite (fig. 7, *B*) is slightly produced and faintly notched at the middle.

The male plates (fig. 7, *D*) are rather slender, broadened at the base, and tapered to bluntly rounded tips. The aedeagus is long, slender, and produced dorsally, and bears a pair of rather long, straight, slender processes at the apex which extend ventrally and laterally (fig. 7, *C*). The pygofer does not bear apical processes.

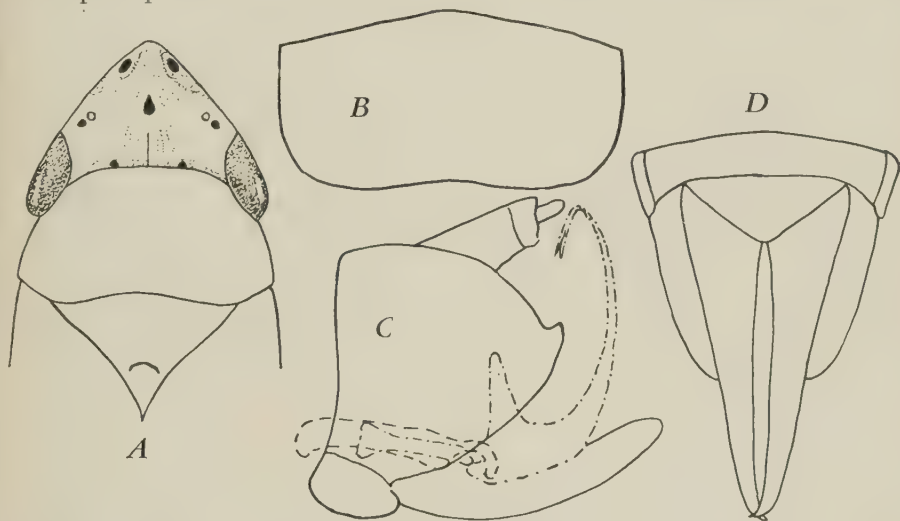


Fig. 7. *Pagaronia confusa* Oman: *A*, dorsal view of head, pronotum, and scutellum; *B*, ventral view of female seventh sternite; *C*, ventral view of male valve and plates; *D*, lateral view of male genital structures.

**Geographical Distribution and California Food Plants.** This species was described from specimens collected at Mount Diablo, California, and has not been collected in other states.

In addition to the type locality, Oman (1938) records the following localities: San Rafael (Oman), Sausalito (Thompson), and Palo Alto (Baker) in California; and Reno (?), Nevada (Brown).

A mixed population of *Pagaronia confusa* and *P. triumata* was collected abundantly by Severin on American vetch (*Vicia americana*) on May 15, 1946, near Atherton, San Mateo County. Adults were also collected on California mugwort (*Artemisia vulgaris*) on May 17, 1946, in Strawberry Canyon, Berkeley, Alameda County.

### PAGARONIA 13-PUNCTATA

**Characters.** *Pagaronia 13-punctata* Ball was described by Ball (1902) and was redescribed as var. *octopunctata* by Kirkaldy (1909). It is 8.0 to 9.5 mm long.

The width of vertex (fig. 8, *A*) between the eyes is slightly greater than its median length.

The color is pale green to yellow. The 13 black spots on well marked specimens are arranged thus: one just below the vertex margin, a pair near the apex above the margin, one anterior to the ocelli on the median line, one below and one behind each ocellus, a pair of smaller ones, often obscure, on the suture just below the ocelli (Ball, 1902), a pair on the posterior margin of the vertex, and three forming a transverse row on the disk of the pronotum. Seven spots on the dorsal side of the head and three on the pronotum are shown in figure 8, *A*. According to Oman (1938), the three pronotal spots, the median spot anterior to the ocelli, and the spots below the ocelli may be inconspicuous or absent.

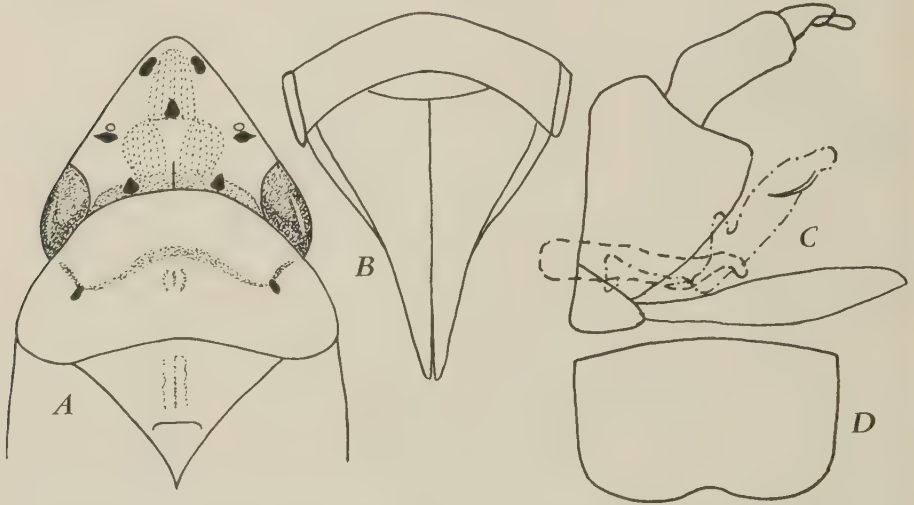


Fig. 8. *Pagaronia 13-punctata* Ball: *A*, dorsal view of head, pronotum, and scutellum; *B*, ventral view of male valve and plates; *C*, lateral view of male genital structures; *D*, ventral view of female seventh sternite.

The posterior margin of the female seventh sternite (fig. 8, *D*) is produced and shallowly notched at the middle.

The male plates (fig. 8, *B*) are elongate, slender, blunt at the apex, and almost three times as long as the basal width. The aedeagus (fig. 8, *C*) is stout, extends dorsally, and has a pair of processes at the tip which are tapered toward the apex, extending ventrally and curved laterally at their apices. The pygofer is plain without spines.

**Geographical Distribution and California Food Plants.** This species is recorded from California only. It is apparently confined to Santa Barbara, Los Angeles, and Orange counties, if we may judge from the known records.

According to Oman (1938) the types of *Pagaronia 13-punctata* Ball are from Los Angeles County (Coquillett and Koebele), Pasadena (Fall), and Marin County (Fuchs). "It is probable that the specimens from Marin County are not *P. 13-punctata* but *P. confusa*." Other localities in which this species was taken are Lancaster (Uhler collection), Mint Canyon, and above Mint Canyon (Oman). Mint Canyon is between Saugus and Palmdale. These records indicate a rather limited distribution in the low hills near Los Angeles.

A single male of *Pagaronia 13-punctata* was collected in California, Santa Barbara foothills (June, 1907) by W. W. Giffard; this was redescribed as var. *octopunctata* by Kirkaldy (1909).

*Pagaronia 13-punctata* was collected by R. C. Dickson commonly on California mugwort (*Artemisia vulgaris*), at Peralta in Santa Ana Canyon, Orange County, on June 7, 1945; and by R. A. Flock in the same locality and in the San Bernardino Mountains, at 4,500 feet.

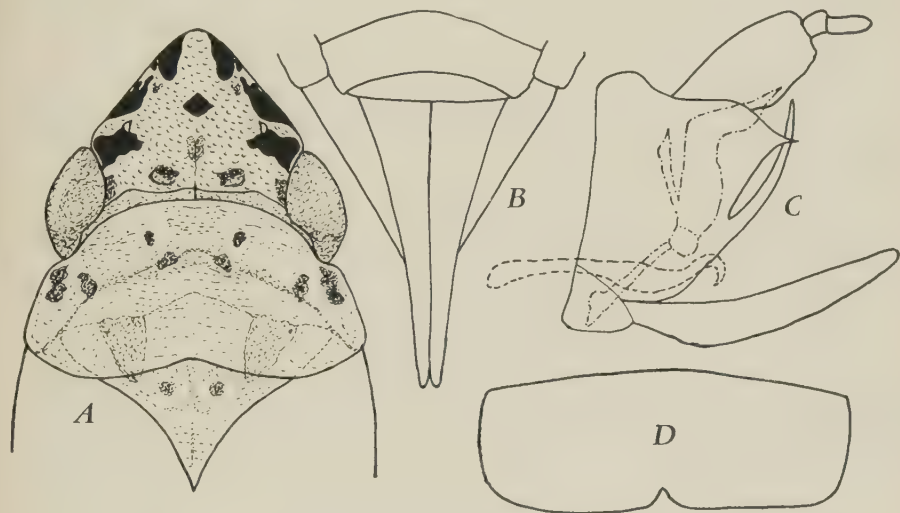


Fig. 9. *Pagaronia triunata* Ball: A, dorsal view of head, pronotum, and scutellum; B, ventral view of male valve and plates; C, lateral view of male genital structures; D, ventral view of female seventh sternite.

### PAGARONIA TRIUNATA

**Characters.** *Pagaronia triunata* Ball was originally described by Ball (1902) as a variety of *P. 13-punctata*. It has since been raised to specific status. The irregular black markings on the head and the slender elongated male plates are distinctive. The length of the male is 7.7 mm, that of the female 9.2 mm.

The width of the vertex (fig. 9, A) between the eyes is a little greater than the median length.

The color is pale dirty yellow. There is a median black spot just beneath the apex of the vertex. Between each eye and the ocellus there is a small black spot, and in front of each ocellus a large irregular black spot which frequently appears bilobate. There is also a small median black spot anterior to the ocelli, an elongate curved spot each side at the base, and a small spot near the base next to each eye. There are black or fuscous markings in the form of spots on the anterior lateral portions of the pronotum. The scutellum contains a pair of minute black or fuscous spots just back of the median anterior margin. The elytra of the male are marked with reddish or reddish-brown cells; those of the female are paler.

The posterior margin of the female seventh sternite (fig. 9, *D*) is slightly produced and has a slight median notch.

The male plates (fig. 9, *B*) are long, slender, nearly parallel-margined, and three times as long as their combined basal width. The apices are bluntly pointed. The aedeagus (fig. 9, *C*) is rather thick, extends dorsally, then is bent caudally. The apex is sharply pointed on the dorsal margin. In dorsal view the apex is bifurcate. The male pygofer is set with two pairs of slender processes. The dorsal pair are short and directed caudally, the ventral pair are long and extend dorsally and slightly caudally almost to the dorsal margin of the pygofer.

**Geographical Distribution and California Food Plants.** *Pagaronia triunata* is known only from California. The type specimens were collected by Coquillett in Santa Clara County, California. Ball (1902) took the species at Salinas, California.

In addition Oman (1938) records the following localities in California: Santa Cruz Mountains (Koebele), Alameda (Van Dyke), Honda (Oman), and specimens in the Uhler collection labeled "Congr.," which presumably means Congress Junction or Congress Springs, both in Santa Clara County.

*Pagaronia triunata* was collected abundantly on grasses growing below pine and oak trees on April 29, May 2, and May 8, 1946, near Atherton, San Mateo County; but not a single specimen was taken on grapevines in a near-by vineyard. After the grasses became dry a few adults were taken on pine trees and on *Acacia baileyana*; they were abundant on American vetch (*Vicia americana*) on May 15, 1947.

## FRISCANUS FRISCANUS

**Characters.** *Friscanus friscanus* (Ball) was described by Ball (1909) as belonging to *Errhomenellus*. Later Van Duzee (1917*b*) described it under the name *Memnonia simplex*. When the group was revised by Oman in 1938, he erected the genus *Friscanus* to include *friscanus*, the genotype.

The female is 5.8 to 6.0 mm long, the male much shorter, 3.8 to 4.0 mm.

The vertex (fig. 10, *A*) is bluntly produced and angled. The width between the eyes is about equal to the median length.

The female is almost uniformly pale green. The male is the same shade, but with a pair of rather heavy longitudinal black stripes across the vertex and pronotum; these stripes are curved and often fused anteriorly. These are sometimes represented by two pairs of spots on the vertex, and fainter markings on the pronotum. The basal angles of the scutellum may be black. Black areas may occur on the claval, apical, and costal cells of the forewings. Black spots are frequent on the dorsum of the abdomen and the tips of the plates.

The posterior margin of the female seventh sternite (fig. 10, *B*) is weakly produced and slightly notched at the middle.

The male plates (fig. 10, *C*) are long and slender, tapering to slightly rounded tips and curved upward posteriorly. The aedeagus (fig. 10, *D*) is rather thick basally. The terminal portion is narrow, pointed, and bent dorsally. The pygofer bears a pair of rather long, slender, pointed, fingerlike processes which arise on the ventral portion and extend dorsally and slightly caudally along the posterior margin of the pygofer.

**Geographical Distribution and California Food Plants.** *Friscanus friscanus* is found rather abundantly in the area around San Francisco but is apparently not widely distributed even in California, and is not known outside this state. The type locality of *Friscanus friscanus* is San Francisco (Ball, 1909). Oman (1938) made extensive collections of this leafhopper from San Francisco or from localities along the coast a short distance south of San Francisco. Nymphs and adults were abundant on *Lupinus arboreus* in June.

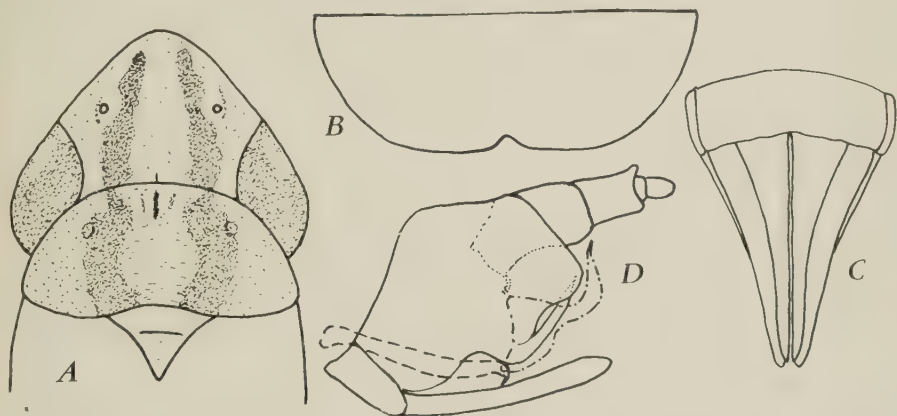


Fig. 10. *Friscanus friscanus* (Ball): A, dorsal view of head, pronotum, and scutellum; B, ventral view of female seventh sternite; C, ventral view of male valve and plates; D, lateral view of male genital structures.

W. W. Giffard collected one male and seven female examples taken at Lands End and Golden Gate Park, San Francisco, in June and July, and in San Mateo County in June (Van Duzee, 1917b).

During the past five years this leafhopper has been collected by Severin on tree lupine (*Lupinus arboreus*) growing along the roadsides near the coast in San Francisco County, and in canyons and exposed slopes of the Montara Mountains in San Mateo County during May and June. During the summer the leafhoppers fly to other plants, and an occasional adult was taken on California sagebrush (*Artemisia californica*).

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# LIFE HISTORY OF THE BLUE-GREEN SHARPSHOOTER, *NEOKOLLA CIRCELLATA*<sup>1</sup>

HENRY H. P. SEVERIN<sup>2</sup>

THE BLUE-GREEN SHARPSHOOTER, *Neokolla circellata* (Baker), is efficient in transmitting the virus of Pierce's disease of grapevines, as shown in the third paper of this issue (Severin, 1949).<sup>3</sup> Its efficiency, its wide distribution (DeLong and Severin, 1949), and its abundance establish it as one of the most important vectors of the virus, especially in north coastal vineyards of California. Since the life history has not previously been reported for this sharpshooter, studies were undertaken on the following aspects: oviposition, egg period, hatching, number of molts, duration of the nymphal stages on grapevines and on alfalfa, and the number of generations under natural conditions at Berkeley in 1943 to 1948. This paper reports the results.

**Oviposition.** Large populations of adults collected in the field during the spring were allowed to oviposit in grapevine cuttings. In the process of oviposition, the female cuts an incision in the petiole, rarely in the midrib, and a single egg is deposited in the slitlike egg chamber.

**Egg Periods.** In the greenhouse, eggs deposited in the petioles during March, April, and May hatched from 16 to 22 days after oviposition.

**Hatching.** Nymphs hatch in the early morning, beginning at 5:00 A.M. during June. During the process of hatching, the nymph, enclosed in the chorion and vitelline membrane, pushes out of the slitlike aperture of the egg chamber. After extrication from the eggshell and embryonic membrane, the nymph remains suspended with the tip of the abdomen in the embryonic envelope, legs sprawled out and the elytra and lower wings held apart. The nymph crawls away after the chitin hardens, and usually settles on the lower surface of the leaf to take its first meal. Sometimes the nymphs experience difficulty in withdrawing the end of the abdomen from the eggshell and membrane. They frequently drop to the ground and then sip moisture from the soil. The dried, shriveled eggshell and vitelline membrane remain in the aperture of the egg chamber.

**Mortality during Hatching.** Hatching is usually completed successfully when early-morning temperatures are between 54° and 68° F. But above this temperature the nymphs push out of the apertures of the egg chambers, fail to rupture the chorion and vitelline membrane, and die.

**Molting.** There are certain indications which appear a day or two before the nymph molts. The body becomes distended, the membranous connections between the head and thorax and abdominal segments become greatly stretched, and the abdomen shows a rounding out.

**Duration of Nymphal Stages.** The interval or periods between molts (stages or stadia) and the total duration of these periods is given in table 1. The average duration of the nymphal stages of this leafhopper is shorter on three varieties of grapevines than on common alfalfa. On grapevines the total dura-

<sup>1</sup> Received for publication May 17, 1948.

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<sup>3</sup> See "Literature Cited" for citations, referred to in the text by author and date.

tion of the nymphal stages of the males averaged 47.0 to 52.7 days, females 46.3 to 51.3 days; and on alfalfa, males 57.6 days, females 66.2 days. On the three varieties of grapevines, one nymph molted 4 times, 21 nymphs 5 times, and 6 nymphs 6 times; and on alfalfa 1 nymph molted 4 times, 17 nymphs 5 times, and 7 nymphs 6 times.

TABLE 1  
DURATION OF NYMPHAL STADIA OF *NEOKOLLA CIRCELLATA*  
REARED ON GRAPEVINES AND ALFALFA

Instar	On Emperor grapevines		On Palomino grapevines		On Ribier grapevines		On California Common alfalfa	
	Males	Females	Males	Females	Males	Females	Males	Females
	<i>days</i>	<i>days</i>	<i>days</i>	<i>days</i>	<i>days</i>	<i>days</i>	<i>days</i>	<i>days</i>
First.....	8-9	7-9	7-10	7-9	7-14	6-10	7-12	7-18
Second.....	6-10	5-7	5-7	5-7	6-9	5-8	3-15	6-13
Third.....	5-27	5-11	5-12	7-12	7-8	5-13	6-26	5-18
Fourth.....	5-7	6-10	7-11	4-12	7-10	4-28	4-16	2-16
Fifth.....	13-27	7-18	11-15	8-19	12-16	10-22	7-26	4-21
Sixth.....	.....	13	13-14	14-17	....	17	17-21	18-28
Total, range.....	39-77	43-50	45-53	43-56	39-54	42-62	43-74	57-85
Average total.....	52.7	46.3	50.5	50.2	47.0	51.3	57.6	66.2

TABLE 2  
AVERAGE MEASUREMENTS OF NYMPHAL INSTARS AND  
ADULTS OF *NEOKOLLA CIRCELLATA*

Stage	Diameter of head across compound eyes			Length of head, thorax and abdomen			Length from head to end of wings		
	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean
	<i>mm</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>	<i>mm</i>
Nymphs:									
First instar.....	0.47	0.61	0.52	1.35	1.72	1.63	.....	.....	.....
Second instar.....	0.68	0.76	0.73	2.08	2.56	2.30	.....	.....	.....
Third instar.....	0.89	0.96	0.93	2.37	3.12	2.75	.....	.....	.....
Fourth instar.....	1.08	1.20	1.15	3.60	4.12	3.83	.....	.....	.....
Fifth instar.....	1.40	1.48	1.43	4.72	5.39	4.90	.....	.....	.....
Adults:									
Males.....	1.48	1.50	1.52	5.60	6.00	6.32	6.20	6.50	6.38
Females.....	1.60	1.70	1.64	6.00	6.80	6.45	6.50	7.20	6.91

**Measurement of Instars.** The diameter of the head across the compound eyes, and the length of head, thorax, and abdomen were measured for each instar. Length from the head to the tip of the wings was also measured for adults. Measurements were made 1 day after hatching and 1 day after each molt. The insects were reared under greenhouse conditions at Berkeley. Table 2 gives the range and mean of the measurements for 10 nymphs of each instar, 10 adult males, and 10 adult females.

Under the conditions used, at least, the ranges for successive instars do not overlap; hence these measurements can be used to determine instars.

Average measurements of the male and female leafhoppers that completed 5 molts show that the males are smaller than the females.

**Color of Nymphs and Adults.** The nymphs (see plate 4, *A, B, C, D, E* in the third paper of this issue) are white with a yellow tinge along the sides of the abdomen.

In northern California, adult males and females are green or bluish green. In southern California they are often bright blue (Hewitt, Frazier, Jacob, and Freitag, 1942). They are yellowish on the ventral surface and have yellow legs. An occasional dark-blue adult was collected in Napa Valley. Baker (1898) in his description of *Neokolla circellata* gives a detailed description of the color pattern and the black marks on the head and thorax (see plate 4, *F, G* in the third paper of this issue).

**Generations.** The number of generations was determined under natural conditions. During 1943, 1945, and 1946, 1 generation occurred in Berkeley; nymphs that hatch in the spring become adults during the summer; the adults winter over, and die the next spring. In 1944 a partial second generation developed on Japanese or Boston ivy, *Parthenocissus tricuspidata*, and on *Statice perezii*. An occasional nymph was taken during the winter of 1946-47 and 1947-48.

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# TRANSMISSION OF THE VIRUS OF PIERCE'S DISEASE OF GRAPEVINES BY LEAFHOPPERS<sup>1</sup>

HENRY H. P. SEVERIN<sup>2</sup>

## INTRODUCTION

FOURTEEN SPECIES of leafhoppers in the subfamily Tettigoniellinae have been reported to transmit the virus of Pierce's disease of grapevines. These species are listed and a number of reports on the virus and its vectors summarized in the first paper of this issue (DeLong and Severin, 1949).<sup>3</sup>

The report (Hewitt, Houston, Frazier, and Freitag, 1946) that the virus causing Pierce's disease of grapevines was identical with that causing alfalfa dwarf stimulated further tests on intertransmission. Frazier and Freitag (1946) reported that ten vectors transmitted virus both from grapevines infected with Pierce's disease to healthy vines and alfalfa, and from alfalfa plants infected with dwarf to healthy vines and alfalfa. These tests, like all others previously reported, were made with multiple lots of vectors, and hence do not furnish data on comparative efficiency. For this purpose, single-insect tests must be used.

In order to find out which vectors were most important, single-insect tests were undertaken in 1942. Efficiency was determined not only for transmission from diseased to healthy grapevines and from diseased to healthy alfalfa plants, but also for intertransmission between grapevines and alfalfa; not all of these tests were made on every vector, however. The present paper reports results with nine of the vectors described in the first paper of this issue (DeLong and Severin, 1949). With two species that proved to be inefficient vectors, multiple-lot tests for transmission were made. Unsuccessful transmission tests with a number of other leafhoppers and a few fulgorids and cicadas are also reported.

Longevity records were kept on three species, and are reported here.

In planning control experiments, it is important to know how soon after acquiring the virus a vector can transmit it to a healthy plant, and how long the vector can continue to transmit the virus after becoming infective. Accordingly, tests were made on the latent period in three important leafhopper vectors of Pierce's-disease virus, and on retention of the virus in the blue-green sharpshooter, *Neokolla circellata* (Baker). Results are reported in this paper. Previous reports on these aspects in the leafhopper vectors of other viruses are summarized for comparison with results on vectors of Pierce's disease.

## METHODS

The method of obtaining noninfective green sharpshooters, *Draeculaphala minerva* Ball, was one first used by J. H. Freitag. Large populations of this leafhopper were collected in the field, and 100 or more adults were allowed to deposit eggs in the leaves of mildew-resistant Sacramento barley,

<sup>1</sup> Received for publication May 17, 1948.

<sup>2</sup> Entomologist in the Experiment Station.

<sup>3</sup> See "Literature Cited" for citations, referred to in the text by author and date.

*Hordeum vulgare*. A few days before hatching, the packets of eggs were dissected from the leaves, and placed on a strip of moist filter paper, one end extending out of the mouth of a phial and the other end submerged in water. The bottom of the phial was embedded in soil in a 6-inch flower pot in contact with barley plants. The nymphs upon hatching crawled on the barley plants, and some completed the nymphal stages, but only a low population of adults was reared.

The method of obtaining noninfective blue-green sharpshooters, *Neokolla circellata*, was similar to that first described by Stahl and Carsner (1918) for the beet leafhopper, and later illustrated by Severin (1921).

Other species of leafhoppers collected in the field were transferred in lots of 20 adults to healthy grapevines or alfalfa plants, to test natural infectivity before using them in vector-efficiency tests in virus transmission. The vines and alfalfa plants served as control plants. The insects were rarely naturally infective. This confirms the results of Hewitt, Houston, Frazier, and Freitag (1946) with *Carneiocephala fulgida* and *Helochara delta*.

The grapevines used were the varieties Emperor, Ribier, Palomino, and Thompson Seedless (*Vitis vinifera*) propagated from indexed cuttings, and wild grapevine (*V. californica*) grown from seeds. Vines grown from cuttings were used in all tests with multiple lots and also in all single-lot tests except in 1943 and 1944, when seedlings were used. The alfalfa was in all cases the California Common variety of *Medicago sativa*.

Details of methods used for specific aspects of transmission tests are given in appropriate sections.

## EFFICIENCY

In the efficiency tests, each species of leafhopper was fed on infected grapevines, and some species also on diseased alfalfa, for 2 days. *Friscanus friscanus* survived only 2 to 6 days on grapevines and 3 to 12 days on alfalfa plants (table 3, page 193), and hence this species was sometimes kept on diseased grapevines for 1 day only. After the feeding period on diseased plants, the insects were transferred singly and kept on healthy plants during adult life.

The following nine vectors were used in single-insect tests for efficiency in transferring the virus of Pierce's disease of grapevines from infected to healthy grapevines:

*Helochara delta* Oman (plate 2,B,C)

Redheaded sharpshooter, *Carneiocephala fulgida* Nottingham (plate 1,A,B)

Green sharpshooter, *Draeculacephala minerva* Ball (plate 1,C,D)

Blue-green sharpshooter, *Neokolla circellata* (Baker) (plate 1,E,F; plate 2,I; plate 4)

*Neokolla confluens* var. *pacifica* DeLong and Severin (plate 3,A,B)

*Neokolla severini* DeLong (plate 2,D,E,F)

*Pagaronia confusa* Oman (plate 3,C,D)

*Pagaronia triunata* Ball (plate 3,G,H)

*Friscanus friscanus* (Ball) (plate 2,G,H,I)

Four of these—*Draeculacephala minerva*, *Neokolla circellata*, *Pagaronia confusa*, and *P. triunata*—were also tested for transfer of the virus from infected grapevines to healthy alfalfa. The numbers and sex of the insects tested and the results obtained are shown in table 1. The blue-green sharpshooter, *Neokolla circellata*, proved to be the most efficient of those tested;

it infected 65 per cent of the 250 grapevines and 35 per cent of 150 alfalfa plants. The species of *Pagaronia* are inefficient vectors: *P. confusa* infected only 6 per cent of 50 grapevines and *P. triunata* none of 50 vines inoculated, and no transmissions to alfalfa were obtained with either species. One infection of alfalfa was obtained with *Draeculacephala minerva*, of 100 plants

TABLE 1  
TRANSMISSION OF THE VIRUS OF PIERCE'S DISEASE OF  
GRAPEVINES BY SINGLE LEAFHOPPERS

Vector	Transferred to healthy grapevines					Transferred to healthy alfalfa				
	Males		Females		Per cent infections, both sexes	Males		Females		Per cent infections, both sexes
	Number tested	Infections	Number tested	Infections		Number tested	Infections	Number tested	Infections	
<i>Heliochara delta</i> .....	50	18	50	14	32	..	..	..	..	..
<i>Carneocephala fulgida</i> ...	50	9	50	24	33 2	..	..	..	..	..
<i>Draeculacephala minerva</i> ...	100	27	100	3	15 4	50	1	50	0	1
<i>Neokolla circellata</i> .....	150	101	100	62	65 1	50	11	100	42	35
<i>Neokolla confluens</i> var. <i>pacifica</i> .....	5	0	1	0	0	..	..	..	..	..
<i>Neokolla severini</i> .....	50	6	50	7	13 6	..	..	..	..	..
<i>Pagaronia confusa</i> .....	25	2	25	1	6	25	0	..	..	0
<i>Pagaronia triunata</i> .....	25	0	25	0	0	..	..	25	0	0
<i>Friscanus friscanus</i> .....	50	4	50	10	14	..	..	..	..	..

TABLE 2  
TRANSMISSION OF THE VIRUS OF ALFALFA DWARF BY  
SINGLE LEAFHOPPERS

Vector	Transferred to healthy alfalfa					Transferred to healthy grapevines				
	Males		Females		Per cent infections, both sexes	Males		Females		Per cent infections, both sexes
	Number tested	Infections	Number tested	Infections		Number tested	Infections	Number tested	Infections	
<i>Draeculacephala minerva</i> ..	100	0	100	0	0	..	..	..	..	..
<i>Neokolla circellata</i> .....	50	0	50	0	0	..	..	..	..	..
<i>Pagaronia confusa</i> .....	25	0	..	..	0	25	0	..	..	0
<i>Pagaronia triunata</i> .....	20	0	25	0	0	..	..	..	..	..
<i>Friscanus friscanus</i> .....	3	0	7	0	0	..	..	..	..	..

inoculated. Because of the scarcity of *Neokolla confluens* var. *pacifica*, only 6 insects were tested, and all were negative. Further tests are needed to establish the efficiency of this leafhopper.

Single-insect tests of transmission of alfalfa dwarf to healthy alfalfa were made with five vectors, and one of these—*Pagaronia confusa*—was also tested for transmission of the virus from infected alfalfa plants to healthy grapevines. The number of insects tested and their sex are shown in table 2. A total of 380 insects was used. As recorded in the table, all tests were negative.

## MULTIPLE-LOT TESTS

Although efficiency can be determined only in single-insect tests, lots of 5 were tested with *Pagaronia triunata* and *Friscanus friscanus*, which proved inefficient in single-insect tests.

Frazier and Freitag (1946), in multiple-lot tests with *Pagaronia triunata*, obtained no transmission of the virus from infected to healthy grapevines, from infected grapevines to healthy alfalfa, or from infected alfalfa to healthy grapevines; but in transfers from infected to healthy alfalfa, 3 of 10 plants were infected. With *Friscanus friscanus*, they transmitted the virus from alfalfa dwarf to 3 of 3 grapevines and 3 of 25 alfalfa plants; no tests of virus from infected grapevines were made with this species.

TABLE 3  
LONGEVITY OF THREE LEAFHOPPER SPECIES ON  
GRAPEVINES AND ALFALFA

Vector	On grapevines		On alfalfa	
	Range	Average	Range	Average
<i>Pagaronia confusa</i> :				
Males.....	5-14	7.8	3-8	5.2
Females.....	2-26	12.2	3-7	7.6
<i>Pagaronia triunata</i> :				
Males.....	4-5	4.2	2-14	5.0
Females.....	4-9	5.4	4-29	7.8
<i>Friscanus friscanus</i> :				
Males.....	2-6	3.6	5-6	5.2
Females.....	2-6	4.1	3-12	7.3

In the present tests with 5-insect lots of *Pagaronia triunata*, 3 infections were obtained with 11 lots transferred from infected to healthy grapevines; and 1 infection in 10 lots transferred from infected alfalfa to healthy vines. No infections were obtained in alfalfa, either from infected alfalfa or from infected grapevines; 10 lots were tested from each host.

With *Friscanus friscanus*, no infections were obtained with 4 lots of 5 adults transferred from infected to healthy alfalfa.

## LONGEVITY OF LEAFHOPPERS

Longevity of adults was determined with *Pagaronia confusa*, *P. triunata*, *Friscanus friscanus*, and *Neokolla circellata*. In the records for the first three species, given in table 3, results on diseased and on healthy plants are not separated; there seemed to be no significant difference. On both hosts the females average somewhat higher than the males; but the longevity is low for all three species on both hosts—a fact which may partially account for the low percentages of infection obtained with these vectors.

Longevity of *Neokolla circellata* is reported in connection with retention of virus in table 7 (page 200). One male lived for 129 days, one female for 92 days on wild grapevine seedlings in the greenhouse. As noted in the second

paper of this issue (Severin, 1949), under natural conditions at Berkeley, adults of this species live from summer of one year to spring of the next. This species has been collected on wild grapevines (DeLong and Severin, 1949) and is probably better adapted to this host than the other three species, whose natural food plants seem to be grasses and weeds, especially legumes.

### SPECIES THAT FAILED TO TRANSMIT THE VIRUS

**Leafhoppers, Subfamily Anthysaninae.** Four species of leafhoppers of the subfamily Anthysaninae that had not previously been reported upon were tested for transmission of the virus causing Pierce's disease and alfalfa dwarf. The species tested and the number of lots used were as follows:

	Lots tested in transfers from:	
	Infected to healthy grapevines	Infected to healthy alfalfa
Beet leafhopper, <i>Eutettix tenellus</i> (Baker).....	6	6
Short-winged aster leafhopper, <i>Macrostes divisus</i> (Uhler)....	12	12
Long-winged aster leafhopper, <i>Macrostes divisus</i> (Uhler)....	12	12
<i>Xerophloea vanduzee</i> Lawson .....	15	15

In addition, *Xerophloea vanduzee* was tested for transmission of the virus from infected grapevines to healthy alfalfa (5 lots) and from infected alfalfa to healthy grapevines (5 lots). In all tests, 20 adult males were used in each lot.

All results were negative. Including tests previously reported, the species in this subfamily that have failed to transmit the virus are:

*Texananus lathropi* Baker (Severin, 1945)  
*Texananus latipex* DeLong (Severin, 1945)  
*Texananus spatulatus* (Van Duzee) (Severin, 1945)  
*Acinopterus angulatus* Lawson (Severin, 1947a)  
*Cloanthanus irroratus* (Van Duzee) (Severin, 1947b)  
*Euscelis maculipennis* DeLong and Davidson (Severin, 1947b)  
 Geminate leafhopper, *Colladonus geminatus* (Van Duzee) (Severin, 1948)  
 Mountain leafhopper, *Colladonus montanus* (Van Duzee) (Severin, 1948)  
 Beet leafhopper, *Eutettix tenellus* (Baker)  
 Short-winged aster leafhopper, *Macrostes divisus* (Uhler)  
 Long-winged aster leafhopper, *Macrostes divisus* (Uhler)  
*Xerophloea vanduzee* Lawson

A large number of other undetermined species of leafhoppers belonging to the subfamily Anthysaninae were tested but none transmitted the virus causing Pierce's disease of grapevines and alfalfa dwarf.

**Fulgorids, or Lantern Flies, Family Issidae.** Since the adults and egg masses of *Hysteropterum severini* (Caldwell and DeLong, 1948) (plate 3, I, J) were occasionally taken on grapevines, an attempt was made to transmit the virus causing Pierce's disease of grapevines and alfalfa dwarf by means of this species of fulgorid. Fifty males and 50 females were kept on diseased grapevines for one day and then each adult was fed on a healthy vine until it died. All attempts to transmit the virus to 100 healthy vines were failures. Negative results were obtained with 20 lots of 5 adults kept on infected grapevines for one day and then transferred to healthy vines and alfalfa plants. The virus was not transmitted by 10 lots of 5 adults fed on infected alfalfa and trans-

ferred to healthy grapevines; or by 20 lots of 10 adults transferred from diseased to healthy alfalfa plants.

This species of fulgorid also failed to transmit the California aster yellows virus from infected celery to healthy celery plants.

The adults of *Hysteropterum severini* were collected on July 2, 1946 on California mugwort, *Artemisia vulgaris*, and on *Brickellia californica*, growing along the banks of the Russian River, near Geyserville, Sonoma County. The adults were commonly taken on olive trees, on coyote brush, or chaparral broom, *Baccharis pilularis*, and occasionally on grapevines on July 2, 17, and 25 near Cloverdale, Sonoma County.

Egg masses were abundant on the trunks and branches of olive trees (fig. 1), occasionally on apple, plum, Oregon oak trees (*Quercus garryana*), poison oak (*Rhus diversiloba*), grapevines, and on fence posts.

Another species of fulgorid, *Neathus maculatus* Melichar, was commonly collected on Parry manzanita, *Arctostaphylos manzanita*, in grape-growing districts of Sonoma County. The transmission of the virus was not accomplished with 50 males and 50 females kept on diseased grapevines for 1 or 2 days and then transferred singly to healthy vines. Twenty lots of 5 adults failed to transmit the virus from Pierce's disease of grapevines to 10 healthy vines and 10 healthy alfalfa plants. The virus was not transmitted by 20 lots of 5 adults fed on infected alfalfa for 2 days and then transferred to 10 healthy vines and 10 healthy alfalfa plants. This species of fulgorid also failed to transmit the curly-top virus.

Some undetermined species of fulgorids failed to transmit the virus causing Pierce's disease of grapevines and alfalfa dwarf.

**Cicadas, or Harvest Flies.** R. Flock carried on extensive tests with undetermined nymphs of cicadas or harvest flies, which survived on the roots of diseased and healthy grapevines for months. No infections were obtained.

### LATENT PERIOD

Since *Neokolla cireclata*, *Carneccephala fulgida*, and *Draculacephala minerva* proved to be three of the most important vectors of Pierce's-disease virus, they were used in determinations of the latent ("incubation") period. *Helochara delta*, another vector, was also used in some tests.

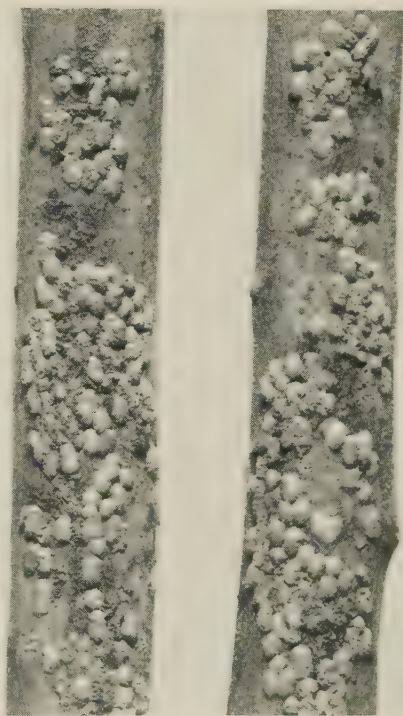


Fig. 1. Egg masses of *Hysteropterum severini* Caldwell and DeLong, deposited on branches of olive trees.

TABLE 4

## LATENT PERIOD OF VIRUSES IN PHLOEM-FEEDING LEAFHOPPERS

Virus and leafhopper species	Authority	Temperature, °F	Adults per lot	Latent period		
				Minimum	Maximum	Mean
Curly top, by beet leafhopper, <i>Eutettix tenellus</i> (Baker)	(Smith and Bonquet (1921). Severin (1921). Carner and Stahl (1924). Severin (1931). Severin (1931). Bennett and Wallace (1938). Freitag (1936).)	103-120 ..... 106-115.6 94 .....	..... 25-50 1 40 1 1 1	24 48 hrs. 4-6 hrs. 2 1/4 hrs. 20 min. 7 hrs. 4 hrs. 1 day	..... ..... ..... ..... ..... 44 days	..... ..... ..... ..... ..... 9.6 days
New York aster yellows, by aster leafhopper, <i>Macrostelus divinus</i> (Uhler)	Kunkel (1926).	70	30-100	10 days	19 days	.....
Eastern aster yellows:						
By aster leafhopper, <i>Macrostelus divinus</i> .	Black (1941).	.....	1	11 days	45 days	.....
California aster yellows:						
By aster leafhopper, <i>Macrostelus divinus</i> .	Kunkel (1932).	70	30-125	17 days	26 days	23 days
By <i>Tezananus lathropti</i> Baker.	Severin (1945).	.....	80	7 days	33 days	13.7 days
By <i>Tezananus latipex</i> DeLong.	Severin (1945).	.....	80	8 days	37 days	22.5 days
By <i>Tezananus spatulatus</i> (Van Duzee).	Severin (1945).	.....	40	6 days	35 days	20.0 days
By <i>Gyponana hasta</i> DeLong.	Severin (1946).	.....	40	19 days	35 days	26.2 days
By <i>Actinopterus angulatus</i> Lawson.	Severin (1947a).	.....	40	11 days	26 days	18.4 days
By geminate leafhopper, <i>Colladonus geminatus</i> (Van Duzee).	Severin (1948).	.....	{ 1 100	31 days 18 days	..... 36 days	31 days 28 days
By mountain leafhopper, <i>Colladonus montanus</i> (Van Duzee).	Severin (1948).	.....	{ 1 100	23 days 8 days	31 days 40 days	27.0 days 23.6 days
Streak of corn (maize), by maize leafhopper, <i>Cicadulina mbila</i> Naude.	Storey (1928).	{ 86 77 60.8	.....	6 hours	63 hours	.....
Peach-yellows, by plum leafhopper, <i>Macropsis trimaculata</i> Fitch.	Hartzell (1936).	.....	4-20	.....	84 hours	.....
Potato yellow dwarf, by clover leafhopper, <i>Aceratagalla sanguinolenta</i> (Provancher).	{ Black (1936). Black (1943).	.....	Many	7 days	26 days	9 days
Dwarf or stunt disease of rice, by rice leafhopper, <i>Nephotettix apicalis</i> Motsch. var. <i>cincticeps</i> Uhler.	Fukushi (1940).	.....	.....	6 days	10 days	.....
Pierce's disease of grapevines, by <i>Draeculacephala minerva</i> Ball.	Hewitt, Houston, Frazier, and Freitag (1946).	.....	.....	10 25 days	60-73 days	30-45 days
		.....	.....	4 days	.....	.....

These species are xylem-feeding insects (Houston, Esau, and Hewitt, 1947). Like all xylem-feeding species, they excrete large quantities of excrement while feeding. When the blue-green sharpshooter, *Neokolla circellata*, was abundant on shrubs and trees in a Berkeley garden, the feces dropping from nymphs and adults resembled a fog.

Until the work on vectors of Pierce's-disease virus began, there had been no reports of xylem-feeding vectors, and no studies on latent period or re-

TABLE 5

LATENT PERIOD OF VIRUS CAUSING PIERCE'S DISEASE OF GRAPEVINES  
IN ADULTS OF THREE SPECIES OF LEAFHOPPERS WITH  
GRAPEVINE CUTTING AS A HOST PLANT

Lot no.	Adults in each lot	Hours on infected grapevine	Successive plants inoculated	Plants infected	Hours on which successive infections occurred including period on infected plant	Latent period, days	Adults alive at end of 7 hours
<i>Carneiocephala fulgida</i>							
1	20	1	6	4	2, 4, 6, 7.....	2	20
2	20	1	6	1	3.....	3	20
3	20	1	6	4	4, 5, 6, 7.....	4	20
4	20	1	6	1	5.....	5	20
5	20	1	6	1	5.....	5	20
6	20	1	6	1	7.....	7	20
7	20	1	6	1	7.....	7	20
<i>Draeculacephala minerva</i>							
8	20	3	11	4	7, 8, 9, 13.....	7	20
9	20	1	13	2	10, 12.....	10	18
10	20	4	10	1	10.....	10	19
11	16	2	12	1	24.....	24	..
<i>Neokolla circellata</i>							
12	5	1	7	4	2, 3, 4, 6.....	2	5
13	5	1	7	3	2, 3, 4.....	2	4
14	5	1	7	4	2, 5, 6, 8.....	2	4
15	5	1	7	2	5, 6.....	5	4
16	5	1	7	1	7.....	7	5

tention of the virus in such insects. However, the length of the latent or "incubation" period of viruses in phloem-feeding species of leafhoppers may be of interest for comparison with that in the three xylem-feeding leafhoppers included in this investigation. These periods, as reported in the literature, are summarized in table 4.

Hewitt, Houston, Frazier, and Freitag (1946) reported that the incubation period of the virus causing Pierce's disease of grapevines in *Draeculacephala minerva*, "if such exists," was less than 4 days.

**Tests on Grapevines.** Lots of from 5 to 20 males were fasted from 1 to 2 hours, and then were kept on diseased grapevines for 1 hour (with a few lots,

2 to 4 hours—see table 5). Hourly transfers were made to successive healthy grapevines for a period of 2 to 13 hours. A total of 16 lots of three species was tested.

As shown in table 5, the minimum latent period of the virus in *Carneoecephala fulgida* and in *Neokolla circellata* was 2 hours, maximum 7 hours; in *Draeculacephala minerva* minimum 7 hours, maximum 24 hours.

Future experiments may demonstrate that the minimum latent period in the three species of leafhoppers may be shorter than 2 hours.

TABLE 6  
RETENTION OF VIRUSES BY SPECIES OF PHLOEM-FEEDING  
LEAFHOPPERS  
(As reported in the literature)

Virus and leafhopper species	Authority	Retention of virus, days
Curly top of sugar beets by beet leafhopper, <i>Eutettix tenellus</i> (Baker).....	{ Bonequet and Stahl (1917)..... Carsner (1919)..... Severin (1924)..... Freitag (1936)..... Wallace and Murphy (1938).....	15-35 58-111* 97-104 1-167 92-121*
New York aster yellows by aster leafhopper, <i>Macrostelus divinus</i> (Uhler).....	Kunkel (1926).....	33-75*
California aster yellows:		
By <i>Tezananus lathropi</i> Baker.....	Severin (1945).....	10-77
By <i>Tezananus latipex</i> DeLong.....	Severin (1945).....	1-42
By <i>Tezananus spatulatus</i> (Van Duzee).....	Severin (1945).....	27-99
By <i>Gyponana hasta</i> DeLong.....	Severin (1946).....	11-46
By <i>Acinopterus angulatus</i> Lawson.....	Severin (1947a).....	51
By <i>Cloanthanus irroratus</i> (Van Duzee).....	Severin (1947b).....	15
By <i>Cloanthanus dubius</i> (Van Duzee).....	Severin (1947b).....	1-29
By <i>Euscelis maculipennis</i> DeLong and Davidson.....	Severin (1947b).....	2-59
By <i>Idiodonus heidemanni</i> (Ball).....	Severin (1948).....	11
By <i>Colladonus comissus</i> (Van Duzee).....	Severin (1948).....	6-27
Streak of corn (maize) by maize leafhopper, <i>Cicadulina mbila</i> Naude.....	Storey (1925).....	84-150
Potato yellow dwarf by clover leafhopper, <i>Aceratagallia sanguinolenta</i> (Provancher).....	Black (1936, 1937, 1943).....	44, 52*, 167†
Dwarf or stunt disease of rice, by rice leafhopper, <i>Nephotettix apicalis</i> Motsch. var. <i>cincticeps</i> Uhler.....	Fukushi (1940).....	53-97

\* Highly resistant or nonsusceptible host plants.

† Hibernating without access to plants.

**Tests on Alfalfa.** Five lots of 20 adult *Carneoecephala fulgida* were kept on alfalfa dwarf plants 1 day and then each lot was transferred daily to six successive healthy alfalfa plants. One lot caused 2 infections during the sixth and seventh days, another lot 1 infection during the seventh day, and three lots failed to transmit the virus to any of the inoculated plants.

In a similar test, 3 lots of 20 adults of *Draeculacephala minerva* failed to transmit the virus from alfalfa dwarf to healthy alfalfa plants.

In a test of *Helochara delta* conducted in the same manner, 5 lots of 20 adults failed to transmit the virus from alfalfa dwarf to successive healthy alfalfa plants.

One lot of 25 *Neokolla circellata* was kept on alfalfa dwarf for 1 day and was transferred daily to 6 successive healthy alfalfa plants. All plants were

infected. Two other lots of 20 adults failed to transmit the virus to any of the plants. Hourly transfers were not attempted on alfalfa.

Further experiments are necessary to determine the minimum latent periods of the virus causing alfalfa dwarf in the first three species of leafhoppers.

### RETENTION OF VIRUS BY THE BLUE-GREEN SHARPSHOOTER

Single adults of the blue-green sharpshooter, *Neokolla circellata*, were tested for retention of the virus from infected grapevines and alfalfa.

As with the latent period, previous reports on retention of viruses concern phloem-feeding leafhoppers. But a summary of these reports (see table 6) may be of interest for comparison with the results with the xylem-feeding blue-green sharpshooter.

Many species of phloem-feeding leafhoppers have been reported to lose their infectivity after varying periods. Ten species of leafhoppers that transmit the California aster-yellows virus lost their infectivity after 1 to 99 days (table 6) (Severin, 1945, 1946, 1947a, 1948). Some species retain the virus over winter. Thus Wallace and Murphy (1938) report that the beet leafhopper, *Eutettix tenellus* (Baker), may retain the curly-top virus throughout the winter without apparent change in virulence; they state, however, that under certain environmental conditions, some specimens lose their infectivity when restricted to a nonsusceptible host plant. Black (1936, 1937) reports that the clover leafhopper, *Aceratagallia sanguinolenta* (Provancher), retained the potato-yellow-dwarf virus for 167 days while hibernating without access to food.

Several species retain viruses, at least occasionally, throughout life. This has been reported of the following viruses and vectors:

Curly-top virus by the beet leafhopper, *Eutettix tenellus* (Baker) (Severin, 1924; Freitag, 1936).

New York aster-yellows virus by the aster leafhopper, *Macrosteles divisus* (Uhler) (Kunkel, 1926).

Streak of corn (maize) by the maize leafhopper, *Cicadulina mbila* Naude (Storey, 1925).

Dwarf or stunt of rice by the rice leafhopper, *Nephotettix apicalis* Motsch. var. *cincticeps* Uhler (Fukushi, 1940).

With most of these species, some specimens lost infectivity before death.

**Tests on Grapevines.** The retention of the virus was determined with single males and females of the blue-green sharpshooter which had completed the nymphal stages on grapevines infected with Pierce's disease. Each adult was transferred daily to successive healthy wild grapevine seedlings until it died. The results are shown in table 7.

The longevity of most of the insects was too short to furnish much evidence on retention. But one male retained the virus 122 days. The male lived 7 days after its last infection; but since the elapsed time between some earlier infections was greater than this, and since infections were as frequent in late adult life as earlier, there is no evidence that this male had lost its infectivity before death. Several females caused infectivity on the last day of adult life, including one female that lived 92 days. Evidently the virus is retained throughout adult life, under greenhouse conditions.

TABLE 7

RETENTION OF VIRUS BY SINGLE ADULTS OF BLUE-GREEN SHARPSHOOTER, *NEOKOLLA CIRCELLATA*,  
WITH WILD GRAPE SEEDLINGS AS A HOST PLANT

Sex and in: ect no.	Plants inoculated	Plants infected		Days on which successive infections occurred	Longest period between two infections, days	Adult age when last infection was produced, days	Period be- tween last infection and death of adult, days	Longevity of adults, days
		Number	Per cent					
Males:								
1.....	129	27	20.9	15, 22, 23, 39, 49, 59, 61, 64, 65, 66, 67, 71, 76, 78, 84, 85, 86, 87, 91, 94, 103, 106, 114, 117, 118, 120, 122.....	16	122	7	129
2.....	50	9	18.0	4, 6, 8, 9, 11, 13, 14, 20, 40.....	20	40	10	50
3.....	36	3	8.4	3, 6, 34.....	28	34	2	36
4.....	31	7	22.6	3, 6, 7, 11, 15, 16, 17.....	4	17	14	31
5.....	32	3	9.4	5, 9, 12.....	4	12	20	32
Av.....	55.6	9.8	15.9	.....	14.4	45.0	10.6	55.6
Females:								
6.....	92	23	25.0	3, 6, 11, 13, 19, 25, 48, 49, 51, 56, 59, 61, 64, 69, 76, 78, 79, 83, 84, 86, 89, 91, 92.....	23	92	0	92
7.....	50	11	22.0	1, 3, 7, 8, 13, 16, 17, 20, 25, 49, 50.....	..	50	0	50
8.....	37	8	21.6	8, 11, 13, 15, 17, 29, 32, 36.....	12	36	1	37
9.....	23	5	17.4	14, 15, 17, 20, 23.....	..	23	0	23
10.....	15	10	66.7	1, 2, 4, 7, 8, 9, 10, 11, 12, 15.....	3	15	0	15
11.....	11	5	45.5	4, 6, 7, 8, 10.....	2	10	1	11
12.....	14	3	..	1, 6, 10.....	4	10	4	14
13.....	9	7	77.8	2, 3, 4, 5, 6, 7, 8.....	0	8	1	9
14.....	9	3	..	1, 5, 7.....	2	7	2	9
15.....	9	5	55.6	1, 2, 3, 5, 6.....	2	6	3	9
16.....	9	5	55.6	1, 2, 3, 4, 5.....	0	5	4	9
17.....	7	4	55.6	2, 3, 4, 5.....	0	5	2	7
Av.....	23.7	8.0	37.9	.....	4.8	22.6	1.5	23.7

Under natural conditions the adults overwinter, and the virus may not be retained during the entire adult life. The investigation furnished no evidence on this point.

**Tests on Alfalfa.** All attempts to determine the retention of the virus by 5 *Neokolla circellata* tested singly in transfers from alfalfa dwarf to healthy alfalfa plants were failures; none of the specimens transmitted the virus.

### ACKNOWLEDGMENTS

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*A**B**C**D**E**F*

Plate 1. Three of the most important leafhopper vectors of the virus causing Pierce's disease of grapevines and alfalfa dwarf: *A*, male, *B*, female redheaded sharpshooter, *Carneocephala fulgida* Nottingham; *C*, male, *D*, female green sharpshooter, *Draeculacephala minerva* Ball; *E*, male, *F*, female blue-green sharpshooter, *Neokolla circellata* (Baker).

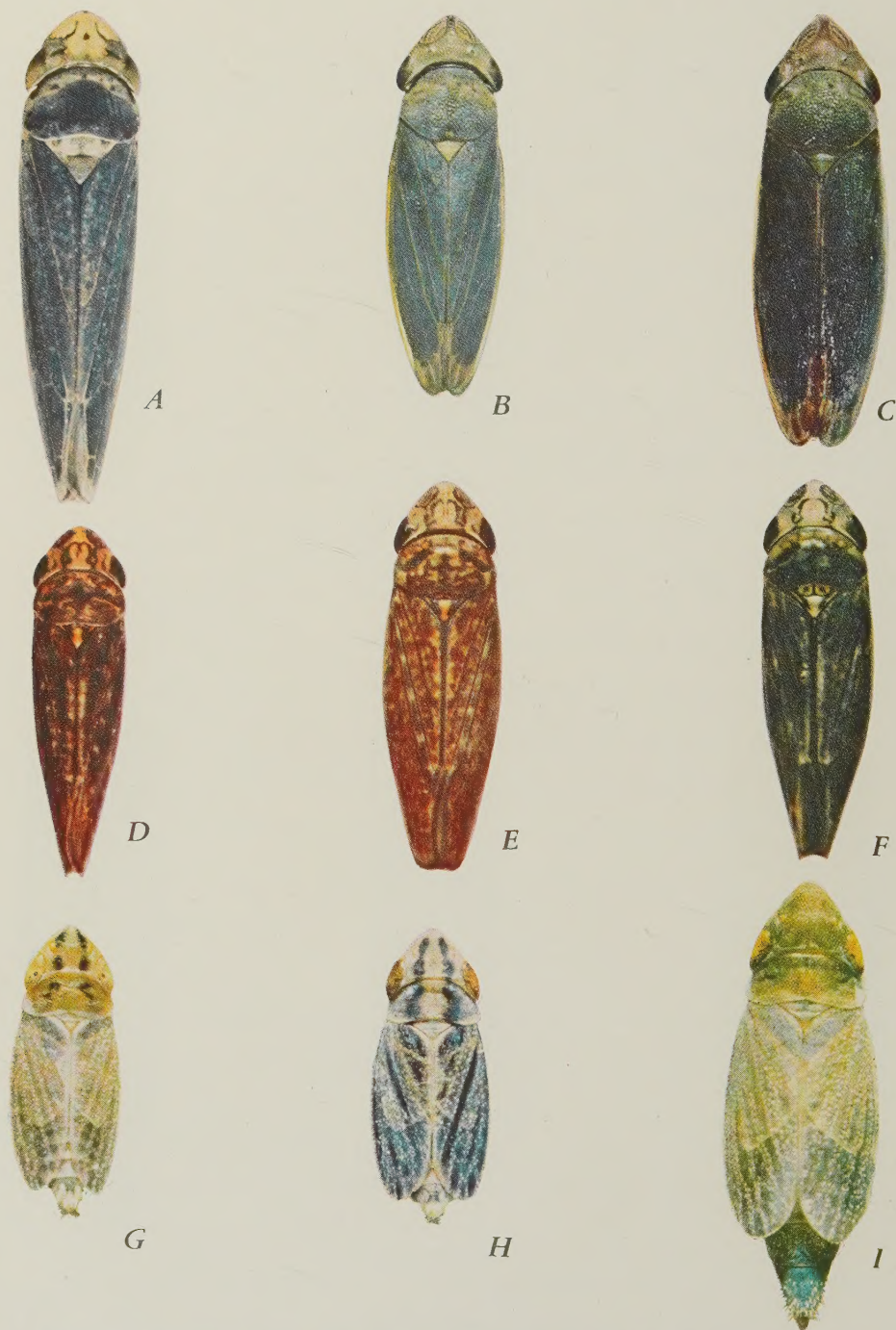


Plate 2. Leafhopper vectors of the virus causing Pierce's disease of grapevines: A, blue-green sharpshooter, *Neokolla circellata* (Baker); B, male, C, female *Helochara delta* Oman; D, male, E, F, female *Neokolla severini* DeLong; G, H, male, I, female *Fricanus friscanus* (Ball).



Plate 3. Leafhopper vectors of the virus of Pierce's disease of grapevines: A, male, B, female *Neokolla confluens* var. *pacifica* DeLong and Severin; C, male, D, female *Pagaronia confusa* Oman; E, male, F, female *P. 13-punctata* Ball; G, male, H, female *P. triunata* Ball; I, male, J, female *Hysteropterum severini* Caldwell and DeLong.



A



B



C



D



E



F



G

Plate 4. Nymphal instars and adults of blue-green sharpshooter, *Neokolla circellata* (Baker): A, B, C, D, E, first to fifth nymphal instars respectively; F, adult male, and G, adult female.